

Instructor's Manual
to accompany
***Animal Behavior*, Ninth Edition**
by John Alcock

Chapter 6: Behavioral Adaptations for Survival

DISCUSSION QUESTIONS

6.1 Many people think that an adaptation is a trait that improves the survival chances of an organism. Under what circumstances would such a trait be an adaptation? Under what other circumstances would a survival-enhancing attribute actually be selected against?

Answer: A survival-enhancing trait would be selected against if individuals with this attribute consistently had even slightly fewer surviving offspring than relatively short-lived individuals.

6.2 Stephen Jay Gould and Richard Lewontin claimed that adaptationists make the elementary mistake of believing that every characteristic of living things is a perfected product of natural selection,⁵⁵⁷ when in reality many attributes of living things are not adaptations (see Table 6.1). Moreover, in their eagerness to explain everything as an adaptation, adaptationists have, according to Gould and Lewontin, invented fables as absurd as the fictional “just-so” stories of Rudyard Kipling, who made up amusingly silly explanations for the leopard’s spots and the camel’s hump. How might adaptationists defend themselves against these charges? Do adaptationists have the means to discover whether their tentative explanations for a particular trait are wrong?

Answer: In science, there are always going to be incorrect, even silly, hypotheses advanced from time to time, although my reading of the animal behavior journals has turned up no truly absurd ones that have managed to get into print. Why not? Because a scientific hypothesis is intended to be tested and without a rigorous test, the hypothesis is very unlikely to be published. Interestingly, Gould and Lewontin picked on a handful of very minor papers, notes really, and they made these examples seem less plausible than they actually were.

6.3 For many evolutionary biologists, the term “adaptation” must be reserved for a characteristic that provides “current utility to the organism and [has] been generated historically through the action of natural selection for its current biological role.”⁸⁴ What could “current utility” mean, and what do you think it should mean? Make use of the terms “fitness benefits” and “fitness costs” in your answer. If a trait originated for function X and later took on a different, but still adaptive, biological role Y, does that mean it is not an adaptation? Track down the

evolutionary history of the flight feathers on the wings of modern birds (see, for example, Prum¹¹⁷²). Where did these feathers come from, and what function did their predecessor feathers exhibit? If you go back far enough in time, will the ancestral form of any current trait have the same function that it does now?

Answer: Current utility could mean a large number of things, ranging from survival-enhancing to body-strengthening but it should mean reproduction-enhancing or gene propagation–improving; in other words, an adaptation is a trait whose fitness benefits must exceed its fitness costs by a greater degree than any alternative form of that trait. Adaptations are measured in terms of their contribution to individual genetic success.

Some of the definitions of adaptations insist on consistency of past and present utility, but every trait, if traced far enough back, will be shown to have antecedents with different functions. Feathers are an excellent example because the flight feathers of today’s birds almost certainly evolved from feathers that served thermoregulatory or display functions, and these feathers in turn evolved from defensive quill-like protuberances from the skin of an extinct reptile. To give a different name to traits whose evolved functions have changed over time would make little sense if all adaptations have had a history of changed function.

6.4 The arctic skua, a close relative of gulls, also nests on the ground and mobs colony intruders, including the great skua, a larger predator that eats a great many arctic skua eggs and chicks. In one study, hatching success and post-fledging survival were greater for arctic skuas that nested in dense colonies than in low-density groups (Figure 6.5); the number of near neighbors was, however, negatively correlated with the growth rate of their chicks.¹¹³³ Rephrase these findings in terms of the fitness costs and benefits of communal mobbing by the arctic skua. If *adaptation* meant a perfect trait, would communal mobbing by arctic skuas be labeled an “adaptation?”

Answer: It appears that nesting in close association with others has some fitness benefits, probably mainly those associated with protection of the young against predators, but there are fitness costs as well, namely those that affect chick growth rate, such as increased competition for food or increased disturbance of chicks by neighboring arctic skuas. If the term adaptation were reserved for traits that were perfect (i.e., had no fitness costs at all), then there would be no attributes of any sort for which the label adaptation was appropriate.

6.5 The ability to hear ultrasound in one species of noctuid moth is considered an antipredator adaptation because it apparently enables individuals to hear and avoid nocturnal, ultrasound-using bats. Imagine that you wished to test this hypothesis via the comparative method. Identify the utility of each of the following lines of evidence about the hearing abilities of other insect species. Specify whether these cases involve convergent evolution, divergent evolution, or neither.

1. Almost all other species of noctuid moths also have ears that respond to ultrasound.
2. Almost all the species in the evolutionary lineage that includes the noctuid moths and many other moths belonging to several other superfamilies also have ears that respond to ultrasound.¹⁶²⁵
3. Some diurnal noctuid moths have ears but are largely or totally incapable of hearing ultrasound.⁵⁰¹
4. Almost all butterflies, which belong to the same large evolutionary grouping as the noctuids but are usually active during the day, lack ears and so cannot hear ultrasound.⁵⁰²
5. Six species of noctuid moths found only on the Pacific Ocean islands of Tahiti and Mooréa have ears and can hear ultrasound but do not react to this stimulus with anti-bat responses.⁵⁰⁵
6. Members of one small group of nocturnal butterflies have ears on their wings and can hear ultrasound; they respond to ultrasonic stimulation by engaging in unpredictable dives, loops, and spirals.¹⁶²⁵
7. Lacewings and praying mantises fly at night and have ears that detect ultrasound and lead to anti-bat defensive behavior (see page 118).

Answer:

- (1) Neither, since this shared feature could be traced to shared ancestry.
- (2) Neither, because this lineage owes its existence to a distant ancestor that may have had ears as well.
- (3) Divergent evolution, because it appears that in the absence of bat predators, a subset of noctuids has evolved a different trait from its nocturnal relatives.
- (4) Divergent evolution, for the same reason as given in (3).
- (5) Divergent evolution, assuming that bats are not found on Tahiti and Moorea, which is the case.
- (6) Convergent evolution, on the grounds that these butterflies almost certainly evolved from diurnal ones that had lost their hearing while these species have regained the trait under selection from bats at night.
- (7) A clear case of convergence with unrelated insects having evolved analogous traits as a result of predation by bats at night.

6.6 Some persons would say that the fact that most noctuid moths have ultrasound-sensitive ears is “simply” a reflection of shared ancestry, a holdover from the past, and therefore that ultrasound sensitivity is not an adaptation in these species.¹⁸² Others disagree, arguing that it makes no sense to define adaptations in a way that limits them to just those traits that have diverged from the ancestral pattern.¹²⁰³ Who is right?

Answer: I find the following argument more persuasive. A trait that has been maintained by selection over time after having evolved in a distant ancestor is a trait that advances individual fitness more than any alternative that has appeared in populations of these species. Thus the mechanism responsible for the persistence of an adaptive trait is no different from the mechanism (natural selection) responsible for the spread of novel

mutant trait that confers greater genetic success on individuals. One could make the distinction between traits maintained by stabilizing selection versus that are spreading because of directional selection (see any evolution textbook) but in either case one can argue that both categories of traits owe their existence to selection and so are adaptations.

6.7 Figure 6.11 shows a nest with a recently hatched black-necked stilt chick and three eggs. A parent has removed most, but not all, of the shell of the egg from which the chick emerged. The adult will be back soon to take the remaining fragment far from the nest. Develop at least one antipredator hypothesis to account for this behavior. List the possible benefits and the likely costs of the parent's actions. Under what circumstances would the benefits probably outweigh the costs?

Answer: One hypothesis is that nests containing broken egg shells are more conspicuous than nests without these egg shells with their white interiors. (Another possibility is that the broken egg shells might scratch or cut the chicks, leading to dangerous infections.) One benefit of the parent's actions based on the first hypothesis is that its youngsters are less likely to be detected, captured, and eaten by visually hunting predators. One cost is that while the parent is flying off with the egg shell, the nest is left unguarded and therefore the young within are more vulnerable to predators. When nesting birds live in areas with many visually hunting predators and have concealed nests and camouflaged offspring, the benefits of removing bright white egg shells may well exceed the costs particularly if the parent is only gone for a short time when carrying the egg shells away.

6.8 In studies of the effect of the spiny water flea, an introduced predator, on *Daphnia*, a small aquatic crustacean once abundant in the Great Lakes, researchers have documented several evolutionary responses. For example, *Daphnia* exposed to spiny water fleas now tend to have larger defensive spines and they also tend to stay in deeper waters away from their enemies. But spinier *Daphnia* move more slowly, and so they secure less food per unit time spent foraging, while deep water *Daphnia* reproduce more slowly because the water is colder. As a result, *Daphnia*'s reproductive rate fell sharply in the Great Lakes,¹¹⁰⁰ leading some to conclude that the evolutionary responses linked to avoiding the introduced predator had done ten times more damage to the population than would have been done if the prey species had remained unchanged and had simply accepted a higher mortality rate from predation. Is this conclusion based on a cost–benefit analysis of the sort we have just been discussing above? Defend your answer.

Answer: The researchers on this project are not using the cost–benefit approach of adaptationists, which focuses on individuals, but instead are thinking about the species as a whole. The implication is that the group would have benefited by not changing in response to the spiny water flea's predation, but evolution by natural selection occurs not for the species' benefit but because of differences among individuals in their hereditary ability to pass on their genes. Even though the selected responses of *Daphnia* have reduced the total population size, individuals that thwarted or avoided predators have left more descendants than those that maintained the once-standard traits of the species. As a

result, group-damaging but individual-benefiting traits have spread through Great Lakes *Daphnia*.

6.9 In my front yard, I sometimes find several hundred male native bees clustering in the evening on a few bare plant stems (Figure 6.15). An assassin bug sometimes approaches the cluster and kills some bees as they are settling down for the night. Devise at least three alternative hypotheses on the possible anti-assassin bug value of these sleeping clusters, and list the predictions that follow from each hypothesis.

Answer:

The dilution effect: Members of a large sleeping cluster should be safer simply because of a lower probability of being killed per night, which would be likely if the predator were to kill only one or two bees per evening.

The fighting back effect: Members of sleeping clusters combine forces to repel assassin bugs, attacking it when it comes to their sleeping places.

The improved vigilance effect: Members of sleeping clusters can react to the presence of an assassin bug by taking advantage of the responses of their neighbors and so flee to safety more reliably.

The actual data support the first hypothesis.

6.10 Consider the following finding: In the years since 1950, pollution controls have reduced the amount of soot deposited on tree trunks, and the melanic form of *B. betularia* has correspondingly become increasingly scarce in Europe,^{163, 294} and North America,⁵⁶⁶ where the species also occurs. Put this statement in the context of a scientific investigation into whether the typical salt-and-pepper coloration of some members of this species constitutes an adaptation. Begin with a research question and proceed through hypothesis, prediction, test, and conclusion.

Answer:

Question: What causes the typical salt and pepper moth to have its speckled appearance?

Hypothesis: That color pattern is an adaptation that reduces predation on resting moths during the daytime.

Prediction: In areas in which the usual resting habitat has become available again after a period of soot pollution of woodlands, then the typical form should become more common again, after a period in which the alternative melanic phenotype was abundant.

Actual results: The data presented above.

Conclusion: Hypothesis supported; the salt and pepper color pattern of the moth is an anti-predator adaptation that evolved in unpolluted woodlands.

6.11 Weiss also collected information on the growth rate of caterpillars that either were forced to inhabit shelters that she contaminated with their feces or were allowed to mature in clean shelters. She found no difference in weight between the pupae that experienced these two different conditions as larvae; moreover, the days required for the larvae to pupate did not differ between individuals growing up with and without waste pellets in their shelters. Why did Weiss gather these data?

Answer: Having demonstrated that the caterpillars were probably safer from wasps as a result of ejecting their feces from their shelters (as described in the text), Weiss also wanted to examine some alternative hypotheses for this waste management behavior. It is possible that the larvae could be infected by pathogens that grew on their waste, thus providing an advantage to individuals that safely disposed of their fecal frass. If, however, this hypothesis were true, then experimental contamination of the living space of the caterpillars should have resulted in sickly, lighter weight, slower growing larvae. Because this was not the case, Weiss could rule out the anti-contamination hypothesis for house cleaning by fecal pellet ejection.

6.12 The Bonaire whiptail lizard (Figure 6.29) runs a short distance from potential predators and then raises one foreleg, which it waves about ostentatiously.²⁹⁶ This arm-waving behavior might be another example of a pursuit deterrence signal. What predictions follow from this hypothesis with respect to when the arm-waving behavior should be performed in response to the approach of a human being (a predator substitute)? That is, should arm waving occur more often when a person approaches slowly or rapidly? In response to a direct or a tangential approach? And which arm should be waved when the lizard is not directly facing the human?

Answer: Slowly approaching potential predators should be signaled in an attempt to short-circuit a really serious attack; rapidly approaching predators require immediate, rapid escape. Likewise, tangential approaches should elicit a signal more than direct approaches because the tangentially approaching predator has evidently not yet decided to mount a full attack. If the arm waving really is a signal to the predator, then the forearm closest to the “predator” should be waved.

6.13 Consider Figure 6.34, a game theory diagram based on the concept of a selfish herd (with thanks to Jack Bradbury). In a population of prey animals, most individuals are solitary and stay well apart from others. But some mutant types arise that search out others and use them as living shields against predators. The mutants take fitness from the would-be solitary types by making them more conspicuous to their predators. We will set the fitness payoff for solitary living in a population composed only of solitary individuals at P . But when a solitary individual is found and used by a social type, the solitary animal loses some fitness (B) to the social type. There is a cost (C) to social individuals in terms of the time required to find another individual to hide behind, and there is a cost arising from the increased conspicuousness to predators of groups composed of two individuals rather than one. When two social types interact, we will say that they each have one chance in two of being the one that happens to hide behind the other when a predator attacks. If B is greater than C , what behavioral type will come to predominate in the population over time? Now compare the average payoff for individuals in populations composed entirely of solitary versus social types. If the average fitness of individuals in a population of social types is less than that of individuals in a population composed of solitary types, can hiding behind others be an adaptation?

Answer: If $B > C$, then the social type will become more common over time. Note that whether a social individual is interacting with another social opponent or a solitary one, it comes out ahead in fitness compared to a rival solitary individual.

The average payoff for a social phenotype in an all-social population is less than that of a solitary phenotype in an all-solitary population. But since an all-solitary population is vulnerable to invasion by a mutant social type (under the conditions specified here), then once that type appears and begins to spread, social behavior becomes the adaptation by definition. The point is that an adaptation can be identified by the higher genetic success of its carriers on average relative to what the other type(s) are *doing in the population*.

QUIZZES

[This section not included in this sample chapter.]

INSTRUCTOR'S RESOURCE LIBRARY VIDEOS

Video 6.1 Mobbing by gulls

In this case, single gulls are shown pursuing and harassing an osprey, a fish-eating hawk that rarely if ever attacks gull chicks or adults. Students can be asked to explain why the gulls are wasting their time and energy in this manner. A possible proximate hypothesis is that the gulls' nervous system is programmed to respond to the visual cues associated with hawks in general, some of which are enemies of young gulls. An ultimate hypothesis is that if gulls were to ignore stimuli associated with hawks, they would enable the true enemies of gulls to search for and find the gulls' offspring or the adults themselves more easily.

(© Cornell Lab of Ornithology, Macaulay Library.)

Video 6.2 Mobbing behavior by rock squirrels

This species is related to the California ground squirrel and is similar in having evolved resistance to rattlesnake venom and in using tail-flagging and sand-kicking to "encourage" a potential predator to leave the area. Students could be asked whether this case provides a comparative test of the proposition that California ground squirrels have evolved tail-flagging and sand-kicking as an anti-predator adaptation against predatory rattlesnakes.

(Courtesy of Don Owings.)

Video 6.3 Leaf mimicry in praying mantids

This video shows different species of well camouflaged insects. Here the students could be asked to predict what the different mantids would do if placed in an arena in which there were different substrates on which to perch.

(Used with the permission of Films for the Humanities and Sciences)

Video 6.4 Alarm calling by avocet

A short video that shows an avocet giving its alarm calls. The video could be used in the context of either Chapter 6 or Chapter 9. Students could be asked to identify the potentially costly nature of alarm calling—as the bird’s signals are obviously loud, presumably easy to locate, and frequent.

(© Cornell Lab of Ornithology, Macaulay Library.)

Video 6.5 Escape behavior of worms in response to mole burrowing behavior

Given that moles feed voraciously on worms, it is not too surprising that worms have evolved a counter-response to their predator. When worms sense the soil vibrations caused by a burrowing mole, they race to the surface in order to escape from their enemy. Bait collectors in Florida have learned to exploit this response by mimicking the stimuli produced by foraging moles; they can then easily collect the worms that flee to the surface.

(Courtesy of Ken Catania)

Students can learn more about “worm grunting” by going to <http://www.plosone.org/article/info:doi/10.1371/journal.pone.0003472>

RECOMMENDED FILMS

Baboon Social Organization. (17 min.) Penn State 21678. Outlines how savannah-dwelling baboons cooperate to repel predators.

Patterns for Survival. (27 min.) Penn State 31421. A film cataloging some remarkable pattern and behavioral adaptations of insects that help them foil their enemies.

Polar Ecology: Predator and Prey. (22 min.) Penn State 20456. The interactions between rodents and predators in the Arctic tundra.

Strategy for Survival. (30 min.) Penn State 32460. An attractive film on the feeding, anti-predator, and migratory adaptations of the monarch butterfly.